



## Mesozooplankton of Shelikof Strait, Alaska: abundance and community composition

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**Abstract**—Zooplankton was sampled in Shelikof Strait and some of the surrounding shelf waters from March to October 1985, and then in Shelikof Strait during spring 1986–1989, using 150 and 333  $\mu\text{m}$  mesh nets. The median integrated abundance of copepods in spring was 1–2 orders of magnitude greater in the Strait (maximum depth >250 m) than over shallower, adjacent regions of continental shelf. Zooplankton fauna was a mixture of oceanic and continental shelf taxa, and among the copepods was strongly influenced by abundance of two deep-water species, *Neocalanus plumchrus* and *Metridia pacifica*. Seasonal development of the copepod community in Shelikof Strait followed similar patterns over the 5-year period. Biomass of copepods showed some large interannual differences related mostly to abundance of the oceanic taxa. Large interannual differences were found for some of the other zooplanktonic taxa as well, but there did not appear to be any correspondence between the patterns shown by these groups and those shown by the copepods. Although euphausiids were not quantitatively sampled, the taxonomic composition and relative abundance and seasonality of species within this group are reported. Copyright © 1996 Elsevier Science Ltd

### 1. INTRODUCTION

Zooplankton was sampled in Shelikof Strait, Alaska and parts of the surrounding shelf as part of an interdisciplinary program investigating environmental influences on the early life history of walleye pollock, *Theragra chalcogramma* (Fisheries Oceanography Coordinated Investigations: FOCI). This boreal Pacific gadid fish spawns in large numbers in the Strait, producing eggs that hatch from late April to middle May (Yoklavich and Bailey, 1990; Kendall and Picquelle, 1990). Most larvae occur in the upper 50 m of the water column (Kendall *et al.*, 1994), where they are both predators (Dagg *et al.*, 1984; Kendall *et al.*, 1987) and prey (Bailey *et al.*, 1993; Brodeur and Merati, 1993) of zooplankton. A taxonomic list of zooplankton from the continental shelf east of Shelikof Strait consists of both neritic/coastal species and an oceanic/slope community (Cooney, 1987). The former is dominated numerically by small- and medium-sized copepods that initiate reproduction in spring and whose populations and biomass increase through the warm months. The

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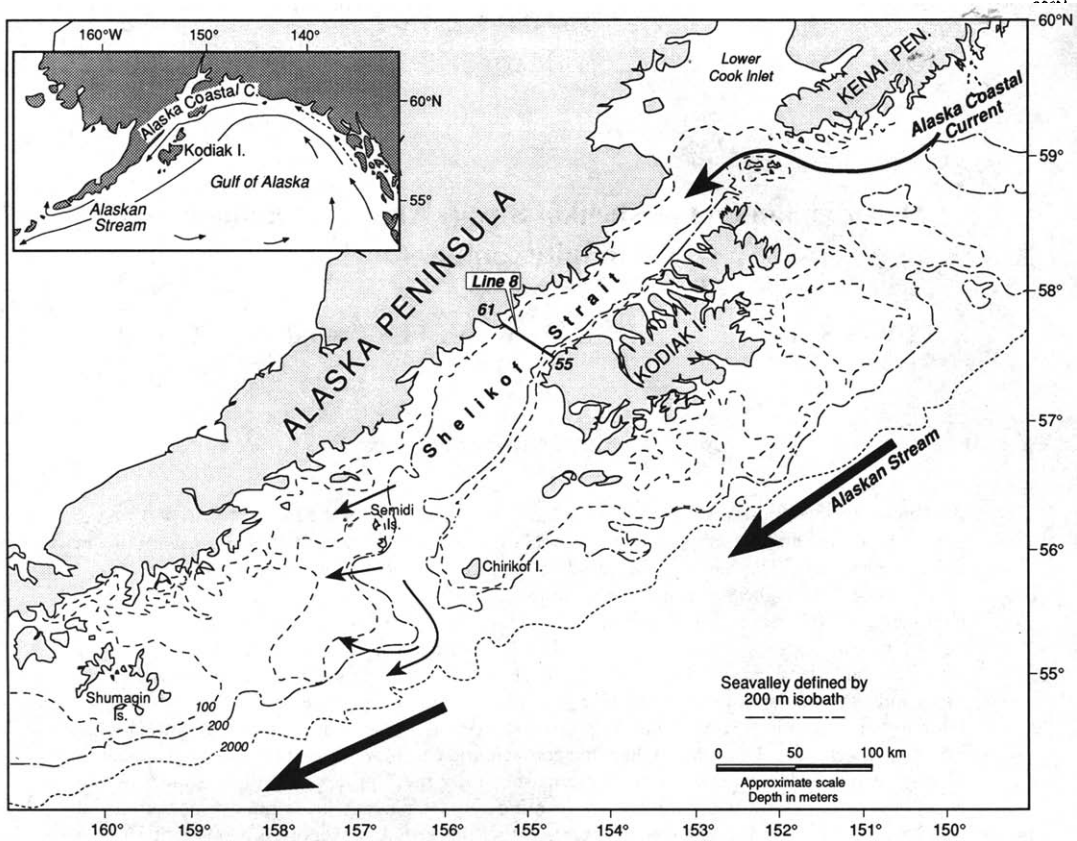


Fig. 1. Study area and schematic of upper ocean circulation. Relative volumes of flow are indicated by widths of arrows in the main panel.

oceanic/slope community includes a mixture of large and small copepods as well as a variety of other abundant holoplanktonic taxa such as euphausiids, chaetognaths, amphipods, pteropods and several gelatinous zooplankton taxa. This community is particularly well known for large and abundant copepods of the genus *Neocalanus* and *Metridia* that have a profound influence on springtime zooplankton biomass of northern Pacific waters (Batchelder, 1985; Cooney, 1986; Vidal and Smith, 1986; Miller and Clemons, 1988).

The predominantly southwestward flow of upper layer water through the Strait is dominated by the Alaska Coastal Current (ACC; Stabeno *et al.*, 1995), which can be distinguished by its higher salinity (Reed and Schumacher, 1989) and has spring-time speeds of  $20\text{--}60\text{ cm s}^{-1}$  (Stabeno *et al.*, 1995). Most of the spring-time transport follows the deep bathymetry at least as far as the Semidi Islands ( $56.3^{\circ}\text{N}$ ,  $156.7^{\circ}\text{W}$ ; Fig. 1), where there may be considerable “leakage” of the upper water column westward on to the shelf. Part of the remaining upper layer flow gets recirculated on to the shelf later, apparently by topographic steering of water moving along the shelf/slope front. In total, about 75% of the surface volume transport of the ACC through Shelikof Strait ultimately reaches the shelf west of the Semidi Islands (Schumacher and Kendall, 1991).

When these studies were initiated in 1985, relatively little was known about

## 2. METHODS

Samples were processed in the authors' laboratory and at the Polish Plankton Sorting and Identification Center in Szczecin, Poland. The joint effort included standardized procedures, cross-training of personnel and verification of results. All data were entered into a computerized database and are available in a series of reports (Siefert *et al.*, 1988; Siefert and Incze, 1989a,b, 1991a,b). The data presented here are for selected taxa and

[illegible]

Table 2. Quantitatively retained copepod taxa and the net mesh size from which they were enumerated

Taxon	Stage	
	333 $\mu\text{m}$	150 $\mu\text{m}$
<i>Neocalanus cristatus</i> *	C6–C2	C1
<i>Neocalanus plumchrus</i>	C6–C3	C2–C1
<i>Calanus marshallae</i>	C6–C3	C2–C1
<i>Calanus pacificus</i>	C6–C3	C2–C1
<i>Metridia pacifica</i> (s.l.)†	C6–C5	C4–C1‡
<i>Eucalanus bungii</i>	C6–C3	C2–C1
<i>Pseudocalanus</i> spp.	C6¶§	C6–C1¶

\*The description of *Neocalanus flemingeri* (Miller, 1988) was published toward the end of this study. We have not distinguished between *N. plumchrus* and *N. flemingeri* in this paper; both species are combined under *N. plumchrus*.

†Thorpe (1980), Dagg *et al.* (1989) and others have pointed to problems with the systematics of northern Pacific *Metridia* spp. We use the name *Metridia pacifica* (*sensu lato*) since our Shelikof Strait females of this genus more closely resemble Thorpe's *M. pacifica* than *M. lucens*, although our examination of specimens has not been exhaustive.

‡C4 are *M. pacifica* (s.l.); C3–C1 are probably *Metridia* spp.

§This mesh analyzed for *Pseudocalanus* spp in 1985 and 1986 only; from 1986 onward we used the smaller mesh samples.

¶C3–C1 are predominantly *Pseudocalanus* spp. (1986–1989) but may contain some copepodites of morphologically similar genera (e.g. *Microcalanus*).

stages that were quantitatively retained (Table 2), by which we mean retention after capture. We assumed that the 333  $\mu\text{m}$  mesh fully retained organisms with a minimum dimension greater than the diagonal measurement of the openings, or 471  $\mu\text{m}$  (Miller *et al.*, 1984). Likewise, we assumed that the 150  $\mu\text{m}$  mesh completely retained organisms larger than 212  $\mu\text{m}$  minimum dimension (but see Siefert, 1994). We compared relative catch efficiencies of the two mesh sizes for selected copepodite stages against predictions based on size and found our predictions for the lower limit of the 333  $\mu\text{m}$  mesh to be functionally accurate for the taxa we report on here.

Numerical abundance of copepods was converted to carbon biomass using average, stage-specific dry weights from published and unpublished sources (Vidal, 1980; Vidal and Smith, 1986; Landry and Lorenzen, 1989; S. L. Smith, unpublished data) and a constant conversion of carbon =  $0.4 \times$  dry weight. *Metridia* biomass was calculated from our measured preserved lengths and Batchelder's (1986) length–weight relationship. *Eucalanus* values were obtained from weights of preserved organisms from our study and corrected according to Vidal and Smith (40% loss). We compare our biomass estimates with data from other regions of Alaska and the North Pacific. Where the latter data were reported in other units (e.g.  $\text{ml m}^{-3}$ ), we converted to carbon units using functional regression equations reported by Wiebe (1988).

Our analyses of these data were constrained by the small number of stations along the transect and by the unreplicated nature of the sampling design. The number of obser-

variations usually was too small to determine if log transformation of data effectively eliminated heteroscedasticity. Therefore, we use station medians as the "least biased" statistic for the central tendency of biomass or concentration along Line 8. Similarly, due to small sample size and unresolved sample variance distributions, nonparametric statistical tests were used for hypothesis testing (Hollander and Wolfe, 1973). Confidence intervals (CI) for the median can be calculated when sample size is greater than seven. When  $n = 7$  (the maximum number of stations on Line 8), the 95% CI for the median is the range of observations (Zar, 1984). Since we did not always sample all seven stations on Line 8, we give confidence intervals only for the broad spatial comparisons of 1985, where  $n > 7$ .

### 3. RESULTS

#### 3.1. Community composition, abundance and development: 1985

There was a *ca* 8-fold increase in the total number of organisms sampled by the 333  $\mu\text{m}$  mesh net from March through October (Fig. 2). Copepods comprised 79–89% of the total.

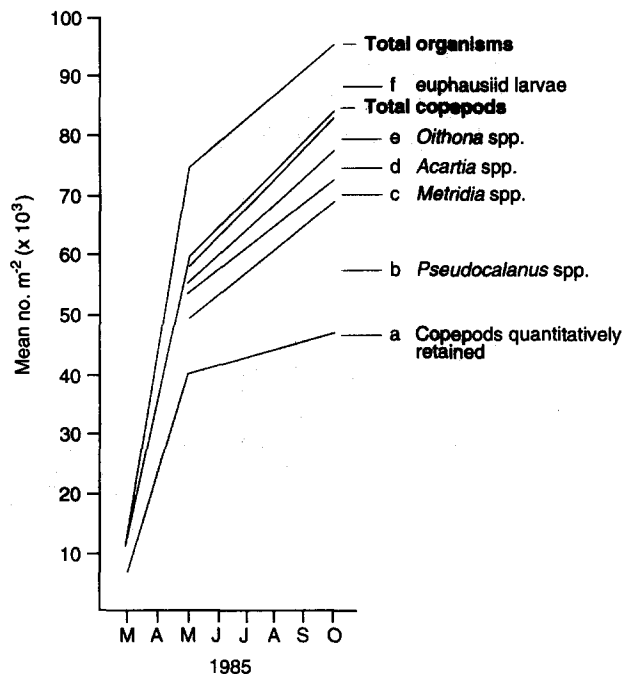


Fig. 2. Abundance of zooplankton sampled by the 333  $\mu\text{m}$  mesh net in 1985. For simplicity, data are shown for March, May and October rather than all months, and some detail is omitted between March and May. Quantitatively retained copepod taxa (a) comprised *ca* 50% of the organisms and are detailed in subsequent figures; the most numerous taxa not quantitatively retained are: (b) *Pseudocalanus* spp. copepodites; (c) *Metridia* spp.  $\leq$  C4; (d) *Acartia* spp.; (e) *Oithona* spp. and (f) euphausiid calyptopes and furciliae (shaded). The narrow unlabeled portion above "e" and the broader portion above "f" are comprised of a mixture of other copepod and non-copepod fauna, respectively.

By our criteria, 55–67% of the copepods sampled were quantitatively retained taxa and stages. We deal first and briefly with a description of the under-sampled groups.

In March, the non-quantitatively retained copepods were mostly C2 stage of *Neocalanus plumchrus* (= *N. plumchrus* + *N. flemingerii*; see first footnote in Table 2) and various stages of Scolecithricidae. From May to October the non-quantitative group consisted mostly of a mixture of stages of *Pseudocalanus* spp. (the numerical dominant, see Fig. 2), *Acartia* spp. and *Oithona* spp., as well as C3 and C4 stages of *Metridia pacifica* (*sensu lato*: second and third footnotes in Table 2). The non-copepod taxa comprised 11–21% of the total organism count. Euphausiid calyptopes and furciliae were the largest single component of this group except in May, when barnacle nauplii were just as abundant.

The rest of the results refer to quantitatively retained organisms unless clearly indicated

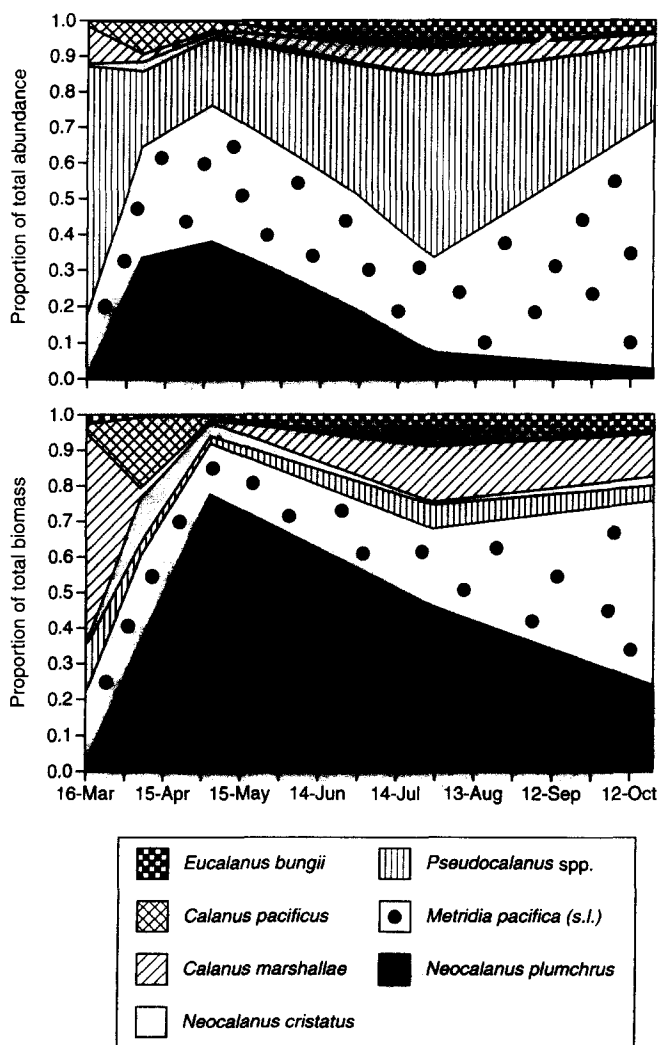


Fig. 3. Taxonomic composition of the quantitatively retained copepod taxa from 1985. Upper panel: proportion by number; lower panel: proportion of biomass comprised by each taxon.

otherwise. We refer occasionally to non-quantitatively retained stages when it is useful to do so.

3.1.1. *Copepods*. *Pseudocalanus* spp., *Metridia pacifica* and *Calanus marshallae* were the numerical dominants in late winter; *Neocalanus plumchrus*, *M. pacifica* and *Pseudocalanus* spp. and *M. pacifica* dominated in fall (Fig. 3). *Neocalanus cristatus* and *Eucalanus bungii* made up only 1.0–7.5% of the copepod numbers, each species being most abundant in the earlier and later parts of the year, respectively. Copepod biomass (Fig. 3) was dominated by *C. marshallae*, *C. pacificus* and *N. plumchrus* during late winter to early spring, by *N. plumchrus* (up to 78%) during spring and summer, and by *N. plumchrus* and *M. pacifica* in autumn. Substantial contributions also were made by *M. pacifica* during summer. *Pseudocalanus* spp. and *E. bungii* each contributed <10% to biomass during summer and fall, when *N. cristatus* contributed less than 3%. The combined biomass of these taxa peaked in May at  $>5 \text{ g C m}^{-2}$ .

Stage composition (Fig. 4) shows that *N. cristatus* and *N. plumchrus* had high springtime (April to May) abundances of copepodite stages C3 and C4 followed by maturation and declining populations; *E. bungii* and *C. marshallae* copepodites were most abundant in summer; and *M. pacifica* were most abundant in fall. *Calanus pacificus* was present mostly as C5 through much of spring to mid-summer, even though there should have been good retention of stages down to C3. *Pseudocalanus* stage composition could not be examined due to limitations of sampler mesh size.

A group of "other copepoda  $>5 \text{ mm}$ " was quantitatively retained but not abundant. Primarily Euchaetidae, the group was less than  $5 \text{ m}^{-2}$  during spring and reached an autumn maximum of  $39 \text{ m}^{-2}$ . Euchaetidae also comprised approximately 10% of a more numerous grouping of unidentified smaller copepods 2–5 mm long which were also quantitatively retained. The abundance of Euchaetidae in both size groups thus is estimated at  $\sim 50 \text{ m}^{-2}$  in spring and  $>200 \text{ m}^{-2}$  in fall. The unidentified copepods 2–5 mm long were dominated by a *Metridia* spp. which ranged in abundance from 450 to  $1690 \text{ m}^{-2}$  from spring to fall. The species in this group was dominated not by *M. pacifica*, but by another species which we did not identify in 1985. Those examined in other years were *M. okhotensis*.

3.1.2. *Euphausiids*. The median abundance of adult and juvenile stages of euphausiids caught in our nets was about  $126 \text{ m}^{-2}$  in March and declined through April and May to 71 and  $6 \text{ m}^{-2}$ , respectively. They increased through July ( $180 \text{ m}^{-2}$ ) and October ( $>455 \text{ m}^{-2}$ ).

*Thysanoëssa inermis* and *T. spinifera* were the most abundant euphausiids in March, each comprising 48% of the total. *Thysanoëssa spinifera* subsequently declined to a much smaller proportion of all euphausiids (3–23%), whereas *T. inermis* remained dominant (70–93%) throughout the period April–October. *Euphausia pacifica* was found on all cruises, but it never exceeded 10% of all euphausiids, which it reached during its own abundance maximum in July. The other species combined, *T. raschii*, *T. longipes*, *T. inspinata* and *Tessarabrachion oculatum*, never included more than 4% of all euphausiids. *Thysanoëssa raschii*, *T. inspinata* and *T. oculatum* were found only during March to May, whereas *T. longipes* was found on most cruises and was most abundant in fall.

3.1.3. *Other holozooplankton*. Gammarid amphipods (*Cyphocharis challengerii*), hyperiid amphipods (*Themisto pacifica* and *Primno macropa*), siphonophores (*Muggia*

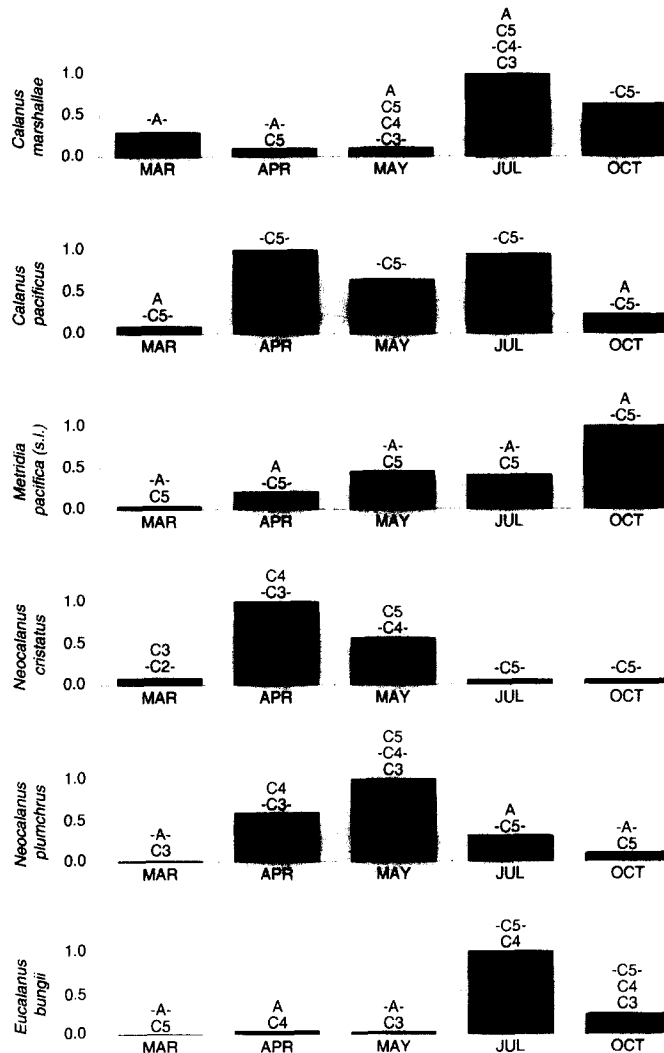


Fig. 4. Occurrence of quantitatively retained developmental stages for copepods, 333  $\mu\text{m}$  mesh, 1985. Stages are listed if they comprised 10% or more of the individuals within a taxon in each of the months shown; stages are abbreviated as "A" (adult) or "Cx" (copepodid stage x). The most abundant stage is enclosed within brackets (e.g. -C3-); no dominant stage is shown for *E. bungii*, March to May, because small numbers precluded a reliable determination. Histogram heights show seasonal changes in abundance relative to the maximum observed for each taxon (e.g. *C. marshallae* reached its maximum in July and declined to 60% of its maximum in October).

Absolute numbers are given in Table 3.

spp.) and mysids (*Meterythrops* spp.) were present at median values  $<100 \text{ m}^{-2}$  during late winter. Chaetognaths (*Eukronia hamata* and *Sagitta elegans*) and cnidarian medusae (mostly *Aglantha digitale*) were at slightly higher late winter levels of about 200 and 300  $\text{m}^{-2}$ , respectively.

During April to May, four of the six groups reached their annual maximum in our sampling: chaetognaths ( $593 \text{ m}^{-2}$ ), mysids ( $509 \text{ m}^{-2}$ ), gammarid amphipods ( $418 \text{ m}^{-2}$ )



and siphonophores ( $252 \text{ m}^{-2}$ ). These groups declined to varying degrees by autumn: chaetognaths to  $419 \text{ m}^{-2}$ , mysids to  $260 \text{ m}^{-2}$  and gammarids to  $62 \text{ m}^{-2}$ . Only siphonophores were completely absent from the October samples. The other two groups reached their maxima after spring. Medusae occurred at their maximum of  $1667 \text{ m}^{-2}$  in July and declined to  $511 \text{ m}^{-2}$  by October, while hyperiid amphipods were at  $1052 \text{ m}^{-2}$  in July and  $1260 \text{ m}^{-2}$  in October.

### 3.2. Spatial patterns

The median abundance of quantitatively retained copepods was much greater in the sea valley than over the relatively shallow bordering shelf regions in March and May, when coverage permitted such a comparison (Fig. 5). In March, *Pseudocalanus* spp., *C. marshallae* and *M. pacifica* copepodites dominated the mesozooplankton of the sea valley and were much more abundant there than on the shelf, although the rank order of the dominant taxa was the same for both areas. Median integrated biomass for the two regions was  $0.80$  and  $0.02 \text{ g C m}^{-2}$ , respectively (corresponding 95% CIs were  $0.42\text{--}1.32$  and  $0.004\text{--}0.394 \text{ g C m}^{-2}$ ). By May, the abundance of these copepod taxa over the sea valley had increased by a factor of about 4–10. The difference in mesozooplankton biomass between the sea valley and shelf in May was less than it had been in March: integrated median biomass was  $4.32$  compared with  $0.55 \text{ g C m}^{-2}$ , respectively (a factor of 8 instead of 40; corresponding 95% CIs of  $3.68\text{--}5.70$  and  $0.22\text{--}2.66 \text{ g C m}^{-2}$ ). The biomass of *C. marshallae* increased from March to May over the shelf ( $4.53$  to  $22.5 \text{ mg C m}^{-2}$ ), but decreased over deeper waters ( $517$  to  $55 \text{ mg C m}^{-2}$ ), where it was replaced by *N. plumchrus* as the second most abundant taxon. In the sea valley the rank order of abundance of the three most abundant taxa was *M. pacifica*, *N. plumchrus* and *Pseudocalanus* spp.; over the shelf it was *N. plumchrus*, *Pseudocalanus* spp. and *M. pacifica*.

### 3.3. Interannual comparisons

The seasonal pattern of development of copepod taxa described for 1985 (Fig. 4) was closely followed in other years to the extent that the seasonal sampling coverage permitted comparison. The carbon biomass of quantitatively retained copepods showed similar springtime patterns in all years, starting at  $\leq 1 \text{ g C m}^{-2}$  in April and increasing rapidly in May (Fig. 6). In the three years with extended sampling periods, biomass declined slightly after an apparent peak in May, but the relative ranking of individual years did not change. Data for 1985 show that the biomass decline closely followed changes in the population of *N. plumchrus*. Among the four years sampled in May, 1986 had the lowest biomass, 1987 had the highest, and 1985 and 1989 were intermediate and similar to each other. We tested for statistical significance of differences among two sets of data that had similar timing with respect to sampling date: 2 May 1985 vs 3 May 1986 (intermediate and low years, respectively) and 18 May 1986 vs 19 May 1987 (low and high years). A Wilcoxon test gave  $P = 0.019$  for the first comparison and  $P = 0.055$  for the second. Table 3 lists the median abundance and the median carbon biomass of copepods arranged by calendar day of year from middle April to middle May, where we have most of our data. By inspection, 1986 stands out in this series as an apparently low year for *N. cristatus*, *N. plumchrus* and *M. pacifica*. The high biomass of middle May 1987 can be attributed to above average numbers of *N. plumchrus* and *M. pacifica*.

Table 3. Spring-time median abundance (No. m<sup>-2</sup>), total median abundance, and equivalent carbon of quantitatively-retained copepod taxa ordered by calendar day of year

Taxon	16 April 1987	26 April 1987	27 April 1988	2 May 1985	3 May 1986	10 May 1989	18 May 1986	19 May 1987
<b>Mesh size = 333 µm</b>								
<i>N. cristatus</i> C6-C2	95	359	599	775	74	197	22	252
<i>N. plumchrus</i> C6-C3	12,415	12,196	18,723	18,302	6064	15,146	5363	30,920
<i>C. marshallae</i> C6-C3	217	1833	932	431	824	6661	13,435	9640
<i>C. pacificus</i> C6-C3	108	442	63	1062	46	371	0	43
<i>M. pacifica</i> (s.l.) C6-C5	7235	14,155	15,983	24,696	9634	12,905	2682	27,375
<i>E. bungii</i> C6-C3	3	9	0	113	3	11	33	13
<i>Pseudocalanus</i> spp. C6 ♀	N/A*	N/A	N/A	(8241)	(13,721)	N/A	(24,691)	N/A
Total (No. m <sup>-2</sup> )†	20,074	28,994	36,299	45,378	16,644	35,290	21,535	68,243
Total carbon (g C m <sup>-2</sup> )†	1.0	3.4	1.9	4.2	1.5	5.2	2.9	12.4
<b>Mesh size = 150 µm</b>								
<i>N. cristatus</i> C1	0	0	0	No net	0	0	0	0
<i>N. plumchrus</i> C2-C1	2854	310	424	"	0	0	0	0
<i>C. marshallae</i> C2-C1	60	1859	3153	"	5023	3988	6744	1718
<i>C. pacificus</i> C2-C1	0	0	0	"	0	0	0	0
<i>M. pacifica</i> (s.l.) C4	2635	4486	9274	"	1811	3018	2836	2446
Metrididae C3-C1	7998	10,175	30,319	"	15,301	17,720	14,376	5064
<i>E. bungii</i> C2-C1	0	0	0	"	0	0	0	0
<i>Pseudocalanus</i> spp. C6-C4	16,503	15,806	36,511	"	51,658	39,430	115,643	96,906
<i>Pseudocalanus</i> spp. C3-C1	27,547	35,373	42,422	"	51,935	22,489	93,489	83,020
Total (No. m <sup>-2</sup> )	57,597	68,009	122,103		125,728	86,645	233,088	189,154
Total carbon (g C m <sup>-2</sup> )	0.2	0.2	0.4		0.5	0.1	1.0	0.8

\*N/A, not counted.

†*Pseudocalanus* spp. C6 females were counted from the 333 µm mesh samples in 1985 and 1986, only. Therefore, they were not included in either Total number or Total carbon.

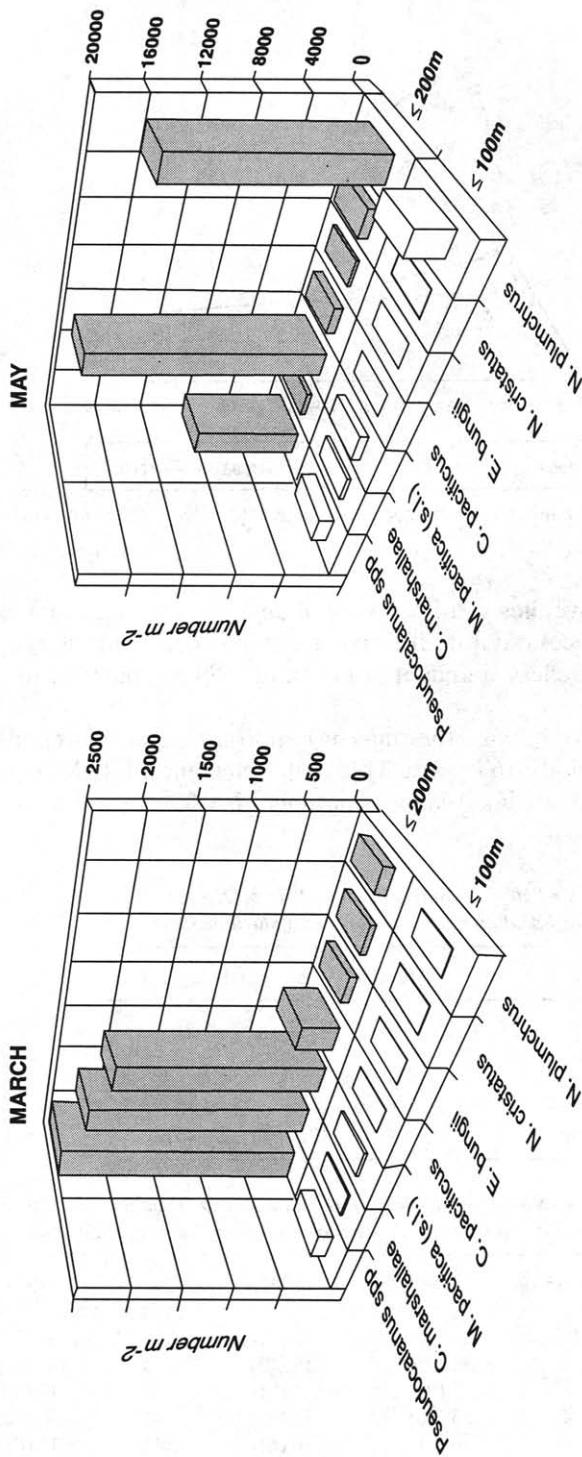


Fig. 5. Spring-time spatial comparison of quantitatively retained copepods in March and May 1985. Histograms show the median integrated abundance ( $No. m^{-2}$ ) by taxon. Depths  $>200$  m are stations in the sea valley; depths  $<100$  m are near the north side of Kodiak Island, on the shelf southwest of the Strait, and on the bank between Kodiak and Chirikov islands (Fig. 1).

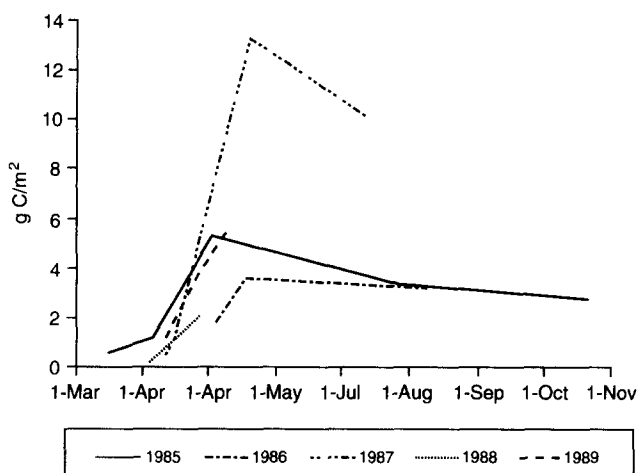


Fig. 6. Biomass of quantitatively retained copepod taxa for all years, 333  $\mu$ m mesh.

Euphausiid adults and juveniles were not very abundant in spring samples (April to May). The median abundances did not differ much among years, but the ranges of data suggest that these stages were less abundant in 1985 and 1988 compared with other years (Table 4).

Other organisms of interest, because they may be important predators of pollock larvae, are grouped for two time periods: 16 April to 3 May (all years) and 10–19 May (three years; Table 5). In the 5-year comparison, 1985 was notably high for several taxa: gammarid

Table 4. Median and range of abundances ( $\text{No. m}^{-2}$ ) of euphausiid adults and juveniles across Shelikof Strait

Date	Median	Range
2 May 1985	6	0–51
3 May 1986	74	6–366
16 April 1987	59	39–260
27 April 1988	28	0–56
26 April 1989	79	24–451

Table 5. Median abundance ( $\text{No. m}^{-2}$ ) of other zooplanktonic taxa. Data are from 16 April to 3 May for all years (early group) and from 10–19 May for three years (late group; in parentheses)

Taxon	1985	1986	1987	1988	1989
Gammarids	418	16 (0)	5 (7)	0	80 (24)
Hyperiid	26	182 (256)	19 (13)	0	150 (87)
Mysids	53	5 (0)	6 (0)	0	12 (20)
Medusae	140	53 (86)	16 (20)	49	56 (42)
Siphonophores	210	0 (0)	10 (6)	42	14 (8)
Total	847	256 (342)	56 (46)	91	312 (181)

amphipods, mysids, medusae and siphonophores. Hyperiid amphipods were comparatively abundant in two years: 1986 and, to a lesser extent, 1989. The two amphipod groups and mysids were absent from our samples in 1988. For the three years that had both early and late sampling periods, within-year differences were not large. A survey of all data in the table suggests that the "zero" observations of 1988 are at least indicative of low abundances.

#### 4. DISCUSSION

Beginning at about 145°W, the ACC courses westward along more than 1000 km of coastline, driven by a strong salinity gradient between offshore waters and freshwater discharge along the coast (Schumacher and Reed, 1980; Royer, 1981; Reed and Schumacher, 1987) and by wind forcing (Johnson *et al.*, 1988). The ACC is confined mostly to within 50 km of shore, and within Shelikof Strait has current speeds typically  $<30 \text{ cm s}^{-1}$  and transport in the order of 0.4–0.6 Sv (Reed and Schumacher, 1989; Stabeno *et al.*, 1995). Before entering the eastern (upstream) end of Shelikof Strait, a portion of the ACC flows over the deep ( $>300 \text{ m}$ ) basin of coastal Prince William Sound. It rejoins the rest of the ACC when it exits the Sound, and it then passes the head of Amatuli Trough ( $>200 \text{ m}$  deep; Royer *et al.*, 1990), which extends from the continental slope to within 40 km of the mainland at *ca* 150°W (Fig. 1). Reed and Schumacher (1987) document slope water intrusions via this trough and follow the resulting salinity signal into Shelikof Strait as part of the coastal flow. Other topographic features also cause complexities in the pattern of circulation, which can enhance across-shelf mixing (Ahlnaes *et al.*, 1987). Because of these dynamics, it is no surprise that the ACC, though it transits the continental shelf, contains large populations of deep-water zooplankton (*E. bungii*, *M. pacifica*, *Neocalanus* spp.). Cooney (1986) suggested that wind-driven convergence along the ACC front may be a major mechanism transporting upper layer oceanic species on to the shelf east of Shelikof Strait (see also Wilson and Overland, 1987). Oceanic plankton also may come from the northeastward bottom flow of slope water that enters Shelikof Strait over the sill (190 m depth) at its western end (Reed *et al.*, 1987), although the volume transport here, usually  $<0.05 \text{ Sv}$ , is about an order of magnitude less than the upper layer (Reed and Schumacher, 1989). Because the northeastward bottom flow enters below about 150 m, its impact on plankton in the upper layer of the Strait would be mostly indirect, as a source of vertically migrating species or stages. This water sometimes can be seen at the surface next to Kodiak Island, but it occupies a narrow band on the eastern side of the Strait. The depth of the Strait and the vertical preferences of zooplankton must play a major role in the geographical distribution patterns shown in Fig. 5. We note, for instance, that *M. pacifica* and *C. marshallae* maintain much stricter differences between Strait and shelf ( $<100 \text{ m}$ ) abundance than either *Pseudocalanus* spp. or *N. plumchrus*. These differences are consistent with data on the vertical distributions of the species and stages involved (Smith and Vidal, 1986; Napp *et al.*, 1996).

By focusing on the quantitatively retained taxa we address only about 60% of the copepods that we sampled, by number, but because of their size this group comprises most of the copepod biomass. Euphausiids unquestionably comprise a major component of the total crustacean planktonic biomass, but estimates of euphausiid abundance and biomass are notoriously problematic because of uncertainty in the efficiency of sampling as well as substantial variations in the weight of individuals (Mauchline, 1980). We do not attempt to

estimate this biomass, but emphasize that these organisms may be an important part of the system in terms of their grazing and their consumption by higher trophic levels. They have been identified as predators on eggs and yolk-sac pollock larvae (Bailey *et al.*, 1993) and they are abundant in the diet of late larval and early juvenile pollock (Merati and Brodeur, in press). Finally, we also should note that we do not estimate the biomass of medusae. While they were not particularly abundant in spring, we encountered impressive numbers of large (up to >0.5 m diameter) *Cyanea* spp. during summer which we did not sample quantitatively.

Our data for copepods over the 5-year period indicate low biomass ( $<1.5 \text{ g C m}^{-2}$ ) in late winter to early spring (March to April) of all years, followed by rapid increases in May, mostly due to populations of *N. plumchrus*, *Eucalanus bungii*, *C. marshallae* and *M. pacifica* become important after the initial vernal increase. In general, the spring-time biomass of copepods inside the Strait exceeds reported values from the subarctic Pacific gyre, Prince William Sound or the nearby coastal waters of Cook Inlet, but is not unlike biomass values from the southeastern Bering Sea during some years (Table 6). Faunistically, the ACC in Shelikof Strait resembles Prince William Sound and the southeastern Bering Sea in that there is a rich assemblage of both oceanic and neritic taxa.

In this study we had one year that stood out for its comparatively high copepod biomass (1987; Fig. 6 and Table 3). This was also reflected in total displacement volume of zooplankton reported by Napp *et al.* (1996). The high biomass of *N. plumchrus* and *M. pacifica* appears to have been a biological property of the ACC in that year and not a function of greater ACC flow through Shelikof Strait. Neither the cross-sectional salinity distribution (Incze and Ainaire, 1994) nor transport (Reed and Schumacher, 1989) appeared unusual. The comparatively low biomass in May 1986 was biologically the converse of the situation noted for 1987: there were low numbers of *N. plumchrus* and *M. pacifica* as well as *N. cristatus*, all indicative of less oceanic influence on the fauna. This, too, is not explained by volume transport estimates (March to May) for the ACC, which are similar for the two years.

There was about 1 order of magnitude difference between high and low abundance years for gammarid amphipods, medusae and siphonophores, all potential predators of yolk-sac larvae and eggs (Brodeur and Merati, 1993; Bailey *et al.*, 1993). The reasons for these variations are not known, but should be of system-wide importance.

Our limited developmental stage data for *C. marshallae* agree with Osgood and Frost (1994), who studied a population in Dabob Bay, Washington (47.5°N). Both populations of *C. marshallae* apparently undergo a single generation per year, with late winter spawning. Osgood and Frost (1994) found that *C. pacificus* in Dabob Bay spawned after *C. marshallae* and had multiple spawnings in the year. We cannot add to Osgood's findings: *C. pacificus* was not abundant in our samples and was dominated by C5, even though we feel we sampled quantitatively down to C3. There appear to have been two generations of *M. pacifica* present in the ACC between March and October 1985, one culminating in the emergence of adults in late spring to early summer and the other marked by the large population of C5 in October. The timing is consistent with Batchelder's (1985) development times of 3–4 months in the central subarctic Pacific, where winter, summer and autumn spawnings occur.

The general patterns of cohort development for *Neocalanus* spp. and *E. bungii* in our study fit the detailed patterns described by Miller *et al.* (1984) and Miller and Clemons (1988) for the central subarctic Pacific and Smith and Vidal (1986) for the southeastern

Table 6. Regional biomass comparison. A comparison of net zooplankton biomass concentrations from other areas of the northern Pacific Ocean

	Month	Sampling period	Biomass (mg C m <sup>-3</sup> )	Depth (m)	Source
<i>Gulf of Alaska*</i>					
Station P	April	1956–1980	1.9‡	0–150	Frost (1983)
	May	1956–1980	2.0		Fulton (1983)
Station 13	Early April	1976	0.6§	0–1500	Damkaer (1977)
	Late May	1976	0.7		
	Early July	1976	1.0		
<i>Prince William Sound*</i>					
	Early April	1976	3.3§	0–700	Damkaer (1977)
	Late May	1976	3.6		
<i>Cook Inlet*</i>					
Kachemak Bay	Early April	1976	0.8§	0–72	Damkaer (1977)
	Early May	1976	17.5		
	Late May	1976	3.7		
	Early July	1976	1.6		
Lower Cook Inlet	Early April	1976	2.2§	0–25	Damkaer (1977)
	Early May	1976	7.5		
	Late May	1976	5.5		
	Early July	1976	20.4		
<i>Alaska Coastal Current</i>					
East of Kodiak Island*	Spring	1978	1.9	0–665	Kendall <i>et al.</i> (1980)
	Summer	1978	2.5		
Shelikof Strait	Late April	1987–1989	11.5¶	0 to bottom	This paper
	Early May	1985, 1986, 1989	21.0		
	Late May	1986–1987	42.8		
<i>Bering Sea†</i>					
Slope	April	1980	1.7**	0–1200	Vidal and Smith (1986)
	May	1980	12.3		
Outer shelf	April	1980	15.4	0–130	
	May	1980	30.8		
Middle shelf	April	1980	21.4	0–70	
	May	1980	21.4		

\*Total biomass of sample.

†Biomass of selected dominant taxa.

Original reporting units: ‡ g WW m<sup>-3</sup>; § ml m<sup>-2</sup>; || ml m<sup>-3</sup>; ¶ No. m<sup>-2</sup>; \*\* g DW m<sup>-3</sup>.

Bering Sea. We used a “cumulative percent regression” technique (Miller and Nielsen, 1988) to estimate the stage duration of C4 *N. plumchrus* in 1985 and derived results (28 days) nearly identical to theirs (25 days for the central Pacific). Our data were obtained from three cruises covering a period of >28 days of flow through the Strait. The high level of consistency in the pattern of development as well as abundance over this time period suggests considerable homogeneity of the population of *N. plumchrus* along >700 km of the ACC (e.g. 30 cm s<sup>-1</sup> for 28 days; cf. Royer *et al.*, 1990; Stabeno *et al.*, 1995).

The ACC clearly is of major importance to the planktonic community present in

Shelikof Strait during spring. It must be important to the broad, shallower region to the west of the Strait as well, because about 75% of the upper layer flow, or upper 100 m, ultimately is retained on the shelf west of 157°W (Schumacher and Kendall, 1991). This pattern of flow transports oceanic taxa such as *N. plumchrus* to areas where it does not occur year round due to the shallow bottom depths. This same transport mechanism brings young-of-the-year pollock and other plankton to this region (Hinckley *et al.*, 1991; Schumacher and Kendall, 1991; Bailey and Spring, 1992). Young pollock, in turn, are important in the diet of numerous piscivores in the region, including birds (Hatch and Sanger, 1992; Piatt and Hatch, in press), marine mammals (Lowry *et al.*, 1989) and other fish (Yang, 1993; Brodeur and Wilson, 1996).

Since the ACC contains meanders and eddies (Myzak *et al.*, 1981; Bograd *et al.*, 1994) that can affect the distribution of planktonic organisms (Vastano *et al.*, 1992; Incze and Ainaire, 1994), we expected that random encounters with such features would superimpose a significant amount of “noise” on the seasonal patterns we were sampling. We also thought that longitudinal (along-axis) differences in the current system might produce erratic changes in zooplankton at our transect site. Instead, details for 1985 show orderly temporal patterns of increasing and decreasing abundance, biomass and development of numerous taxa. A comparison of all years suggests similar patterns for the aggregate value of total biomass. Finally, the “early” and “late” groupings of other zooplanktonic taxa (Table 5) showed greater consistency than we had reason to anticipate. Some of the apparent smoothness of these temporal trends may be an artifact of the scale of observation. We did not focus on the mesoscale in this study, and the within-year sampling periods often were too far apart temporally to reflect short-term variability (i.e. in 1985, 1986). Others that were closer in time, however, also provide no evidence of major fluctuations among them: in 1987, 1988 and 1989 there were three samplings each year within a period of 4–6 weeks (Table 1; also see groupings in Table 5). We can think of two reasons, outside of pure chance, why these relatively uncomplicated patterns occurred. First, baroclinic instabilities usually occupy only about one-half of the 50 km wide Strait. Consequently, upper layer water associated with the ACC usually can be found somewhere in the transect, and deeper water may be displaced very little. Second, much of the dynamic structure associated with these features is in the ACC itself, thereby not involving a second water type (such as coastal water) and its associated biota (Incze and Ainaire, 1994). Differences in the current system surely occur along its length, but it appears that the processes that transport plankton to Shelikof Strait integrate these differences sufficiently that seasonal and ontogenetic changes dominate the data. We conclude that the single transect across Shelikof Strait, integrating the water column and repeating a few times during spring, provides a reasonable measure of the background planktonic community in the ACC at this point in its course. We suggest for the future that the transect be accompanied by upstream and downstream hydrographic transects that can help determine the dynamic baroclinic setting of the samples.

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